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Testing a general approach to assess the degree of disturbance in tropical forests

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Abstract

Questions: Is there any theoretical model enabling predictions of the optimal tree-size distribution in tropical communities? Can we use such a theoretical framework for quantifying the degree of disturbance?

Location: Reserve of Yangambi, north-eastern region of the Democratic Republic of Congo.

Methods: We applied an allometric model based on the assumption that a virtually undisturbed forest uses all available resources. In this condition, the forest structure (e.g. the tree-size distribution) is theoretically predictable from the scaling of the tree crown with tree height at an individual level. The degree of disturbance can be assessed by comparing the slopes of the tree-size distribution curves in the observed and predicted conditions. We tested this tool in forest stands subjected to different degrees of disturbance. We inventoried trees>1.3 m in height by measuring the DBH in three plots of 1 ha each and we measured tree height, crown radius and crown length in a sub-sample of trees.

Results: All tree species, independently of the site, shared the same exponents of allometric relationships: tree height *vs.* tree diameter, crown radius *vs*. tree height, crown length *vs.* tree height and consequently crown volume *vs.* tree height, suggesting that similar trajectories of biomass allocation have evolved irrespective of species. The observed tree-size distributions appeared to be power laws (excluding the finite-size effect) and, as predicted, the slope was steeper in the less disturbed forest (-2.34) compared to the most disturbed (-1.99). The difference in the slope compared to the theoretical fully functional forest (-2.65) represents the metric for assessing the degree of disturbance.

Conclusions: We developed a simple tool for operationalizing the concept of "disturbance" in tropical forests. This approach is species-independent, needs minimal theoretical assumptions, the measurement of only few structural traits and requires a low investment in equipment, time and computer skills. Its simple implementation opens new perspectives for effectively addressing initiatives of forest protection and/or restoration.

Keywords: crown volume; allometric relationships; finite-size scaling; operationalization; restoration strategies; tree-size distribution; tropical ecology.

Running head: How to operationalize the term "disturbance"

Abbreviations:

B = tree metabolic rate;

CDF= Cumulative Distribution Function;

DBH = tree diameter at breast height;

EDG = Plot within an old-growth forest subject to edge effect;

h = Tree height;

H = scaling exponent of crown radius *vs.* crown length;

JEU = Plot within a relatively young regrowth forest;

l_{cro} = Crown length;

MIX = Plot within an old-growth mixed forest;

r = tree diameter at the stem base;

r_{cro} = Crown radius;

V_{cro} = Crown volume.

Introduction

Tropical forests are a key biome in controlling planetary carbon stocks and fluxes, water cycles, biodiversity and global climate patterns whilst also providing ecological, economic and social services (Lewis 2006; Lewis *et al*. 2009; Slik *et al*. 2015). However, they are under severe threat and major discussions are underway to determine the exact rates of forest loss and degradation (Hansen *et al.* 2013; Achard *et al*. 2014; Kim *et al*. 2015). Forest losses are essentially driven by human population growth that requires more cultivated lands and pastures to improve food security and by numerous economic interests such as palm oil plantations and timber extraction (Sayer *et al*. 2012; Wilcove *et al*. 2013; West *et al*. 2014; Carrasco, Larrosa & Edwards 2014; Lewis *et al*.2015). This trend will continue as long as conservation strategies remain less appealing than what private companies can offer to forest-dwelling communities (Novotny 2010).

Assessments of whole forest functionality and the degree of disturbance are essential for defining strategies for specific forest management and restoration activities. The UN Framework Convention on Climate Change, UN Food and Agriculture Organization (FAO), UN Convention on Biological Diversity (CBD) and International Tropical Timber Organization (ITTO) have different definitions of "disturbance". This is generally defined as a discrete event in space and time that affects forest functionality, structure, species composition, canopy cover and carbon stocks. Assessing variations in forest structure or canopy cover rely on a combination of remote sensing technology and field studies. However, forests can undergo subtle changes that remote sensing is unable to detect, such as non-mechanized and small scale logging and cryptic effects of climate change (Peres *et al.* 2006; Goldstein 2014). Field studies require a lot of time and human resources, and still need a set of

110 recognized metrics providing specific information about disturbances (Nagendra
111 2012; Ghazoul *et al.* 2015). Consequently, the assessment of "disturbance" is
112 nowadays ruled by uncertainty, especially in the tropics.
113 Our aim is to partially fill this gap by applying a species-independent allometric tool
114 that, differently from other more sophisticated and complex models (e.g. forest gap
115 models; Bugmann, 2001), can easily predict the slope of the tree-size distribution
116 relative to a "fully functional" forest (i.e. a forest which uses all available resources).
117 Thus any deviation from this predicted distribution can be interpreted as metric of
118 disturbance.
119 A similar allometric approach was already proposed by Kerkhoff, & Enquist (2007),
120 who demonstrated that systematic departures for the (universal) expected allometric
121 relationships might be used as an indication of perturbation processes both in forest
122 ecosystems and in human settlements size. We further developed this idea by using
123 the "*H-model"* (Simini *et al*. 2010; Anfodillo *et al*. 2013) that, contrary to the
124 approach of Kerkhoff & Enquist (2007), is characterized by different allometric
125 relationships (i.e. the scaling exponent of the DBH distribution can assume values
126 different from -2). The expected exponent characterizing the tree-size distribution is
127 estimated by the scaling of the tree crown with tree height at an individual level. We
128 believe this scaling to be independent of specific and episodic disturbance (i.e.
129 harvesting, wind, fire) because natural selection favoured only a limited set of scaling
130 relationships, determining plant structure.
131 We already tested this tool successfully in temperate forests (Anfodillo *et al*. 2013)
132 and in a virtually undisturbed tropical forest (Simini *et al.* 2010). Here, we further test
133 the capacity to assess the degrees of disturbance in tropical communities in the Congo
134 basin by selecting three different forests in which the disturbance regime was

relatively well known (i.e. an old-growth mixed forest, a young regrowth forest and old growth forest undergoing edge effects).

In summary, we tested the following hypotheses: i) allometric relationships at the tree level are species-independent and unrelated to the degree of forest disturbance and; ii) disturbances lead to systematic deviations from allometrically predicted tree-size distributions with a shallower slope in the most disturbed forests and a steeper slope in the less disturbed forests. This deviation represents the metric of forest disturbance.

Material and Methods

Study area

The study plots are situated in the UNESCO Man and Biosphere reserve of Yangambi in the north-eastern region of the Democratic Republic of Congo between 0° and 1° N latitude. The area has an Af-type tropical rain forest climate (Peel *et al.* 2007) with mean annual precipitation of 1,762 ± 295 mm (1961-2010) (Kearsley *et al.* 2013). It has a dry season from January to February with a minimum precipitation of about 100 mm per month (Hijmans *et al*. 2005). The highest and lowest temperatures are in March (25.5 ± 0.6 °C) and July (24.2 ± 0.4 °C) respectively. The soil is a Ferralsol with aeolian sediments, mainly composed of quartz sand, kaolinite and hydrated iron oxides (Van Ranst *et al*. 2010; Gilson *et al.* 1956).

The COBIMFO project established the plots in 2012 (Kearsley *et al.* 2013). Each plot was 1 ha of a square (100x100 m with subplots of 20x20 m) or rectangular shape (50x200 m with subplots of 25x25 m). COBIMFO researchers tagged, identified to species and measured at breast height (*DBH*) each tree ≥10 cm in diameter. In terms of forest disturbance, the main difference among the plots was due to human activity. The local communities practice slash-and-burn agriculture, including clearing after burning and cultivation until the soil loses fertility; the fields are then left uncultivated for up to 20 years to allow soil regeneration (De Wasseige *et al*. 2012).

In total we sampled three hectares of forest that were divided in three plots: one plot of old growth mixed forest (MIX plot), one of relatively young regrowth forest (JEU plot) and one of old growth forest subject to edge effects (EDG plot). The old-growth forest contains more than 70 species per ha (Table 1) with dominance of para-climax, long-living, light-demanding species such as *Prioria oxyphylla* [(Harms) Breteler] or *Pericopsis elata* [(Harms) Meeuwen] (Gilson *et al*. 1956) and shade tolerant species

such as *Scorodophloeus zenkeri* (Harms). The old-growth forest (MIX) could be defined as "virtually undisturbed" according to the work of Lebrun & Gilbert (1954), Gilson *et al*. (1956) and the field knowledge of guides and local communities but the presence of *Pericopsis elata* (a light-demanding species) might suggest that the MIX plot has been slightly disturbed many decades ago (see below for comments). The regrowth forest (JEU) was about 10 years old, but with some bigger trees that had survived the slash-and-burn practice. This forest is characterized by fast-growing and light-demanding species (e.g. *Musanga cecropioides* R. Br. ex Tedliee, *Macaranga spinosa* Muell.Arg.). The understory was tightly filled with herbaceous species and trees were more dispersed than in the old growth plot. The old growth plot undergoing edge effects (EDG) was of rectangular shape; its shorter side was along the forest boundary, adjacent to cultivated fields. The harvesting outside the plot had been done about 5 years before the sampling.

Dendrometric data

In addition to the measurements already done by the COBIMFO Project, we measured tree height (i.e. top leaves), crown radius and crown height on approximately 100 individuals >10 cm DBH per plot. We tried to record the widest possible range of heights. These data were used to estimate the value of the *H* exponent (see below), which drives all other allometric relationships used. We also measured total height, crown radius (r_{cro}), tree height (and, consequently, crown length, l_{cro}) and *DBH* of all living trees above 1.3 m and <10 cm in diameter in two randomly selected 20x20 m subplots within each plot. We measured *DBH* with calipers (mean of two perpendicular measurements), tree height (*h*) with a Tru-Pulse 200B laser rangefinder (Laser Technology Inc., Centennial, CO, USA) or with a measuring tape for young

193 individuals and r_{cro} with a measuring tape. We measured a total of about 1500 small
194 individuals across all six 20x20m subplots.
195
196 *Model structure and implementation*
197 The *H-model* allowed us to determine the slope of the tree-size distribution curve of
198 the "fully functional" forest (i.e. a forest able to use at maximum the available
199 resources) from the scaling of crown volume with tree height at an individual tree
200 level. Details on the structure of the model and the main assumptions are given in
201 Anfodillo *et al.* (2013) and Simini *et al.* (2010): here we summarize the three
202 necessary steps for basically understanding and applying the model.
203 i) *Metabolic rate in individual trees*: as in other allometric approaches (e.g. West *et al.*
204 2009) the metabolic rate of an individual tree (B) is assumed to be linearly related to
205 leaf area and, therefore, to crown volume (V_{cro}) (assuming constant crown density
206 with ontogenesis; see discussion for comments). The use of resources (i.e.
207 productivity) of a single tree depends on its V_{cro}. V_{cro} is assumed to scale as $l_{cro}*r_{cro}^2$,
208 where l_{cro} is the crown length and r_{cro} is the crown radius. The formula simplicity does
209 not affect the scaling exponent, as we are interested in the relative change in crown
210 volume with respect to height. Thus, the same scaling exponent is obtained even when
211 considering more convoluted formulas to describe crown volume. This approach
212 ensures a good estimation of scaling of B with respect to tree height (h), as we are
213 interested in the relative change of V_{cro} with h and not its absolute variation.
214 Assuming that 1) the $r_{cro} \propto l_{cro}^H$ and 2) the $l_{cro} \propto h^a$ (a is a newly introduced parameter
215 that allows for the possibility that l_{cro} might scale with h with an exponent larger than
216 1, see discussion), the relationship linking V_{cro} with h is therefore $V_{cro} \propto l_{cro}^{1+2H}$
217 $\propto h^{a(1+2H)} \propto B$.

When a=1 and H=1 then $V_{cro} \propto h^3$ as in the West *et al.* (2009) model. Note that, due to geometrical constraints, the *maximum* value of H is assumed to be equal to 1 but lower values are possible (see discussion). The case of exponent $H=1$ and $a>1$ (i.e. a=1.11) was found in trees growing in the Yangambi forest yielding $V_{cro} \propto h^{3.33}$.

ii) *Finite size scaling*: the tree-size distribution curve is not a pure power law (Maritan *et al.* 1996), as shown, for example, in Fig. 2 (grey dots). The behaviour of the log-log tree-size distribution curve is linear (black dots) until a certain threshold. Naturally, physiological constraints and lack of resources limit the maximum height of trees in an ecological community. The scaling theory takes into account the finite range of tree sizes by introducing an upper cut-off to the pure power law behaviour. The upper cut-off identifies the so-called characteristic height (h_c) or diameter (r_c) and it sets the maximum value for correctly fitting any tree-size distribution curve (Stanley 1999). There is also a lower cut-off. While the upper boundary to power law behaviour is due to resource limitations the lower one is experimentally biased because it is impossible to measure all very small plants (seedlings) in a given area (some may be hidden, others might have died just after emergence). The two cut-offs are estimated by selecting the range of values that maximizes the r^2 of the linear regression.

iii) *Community use of resources*: the model assumes that a virtually undisturbed forest is able to use all the available resources in a given site. Therefore, the metabolic rate of the community (i.e. the gross primary productivity) is *proportional* to the amount of leaves filling the volume, that is $A*h_c$, where A is the area of the forest and h_c the characteristic tree height (i.e. the upper limit of the power law regime). It derives that

the productivity is clearly higher in sites where resources are greater because h_c is also greater. In this condition we can easily demonstrate (Simini *et al.* 2010; Anfodillo *et al.* 2013) that the probability, $P(h_i)$, of finding a tree of a given size h_i scales inversely with the metabolic rate (B_i) of that particular size or, analytically, that

$-dP^{>}(h|h_c)/dh \propto 1/h^{a(1+2H)}$ corresponding to $-dP^{>}(h|h_c)/dh \propto B^{-1}$

Thus, when h is used as metric for tree-size distribution it follows exactly the Energy Equivalence Rule proposed in animals (Damuth 1981), which states that density (N per unit of area) of individuals of a given species scales inversely with the average metabolic rate of the species (i.e. $N \propto M^{-0.75}$ or $N \propto B^{-1}$). Importantly it follows that the scaling of metabolic rate at tree level drives the structure of the whole community or, equivalently, that the tree architecture sets the structure of the whole forest. If tree height is used as metric for describing the tree-size distribution curve then the relationships come directly as mentioned above (e.g. $N_{max,hc} \propto h^{-a(1+2H)}$) and, in the specific case, when a=1.11 and H=1 then $N_{max,hc} \propto h^{-3.33}$, where $N_{max,hc}$ is the number of trees of height h in the domain between the two cut-offs under the condition of full resources use. However, in dense forests it is very difficult to measure the height of all trees. The *DBH* (or the diameter at stem base, r) can be used as an alternative but a variable transformation becomes necessary. In this specific case, the full resource use condition will predict a tree-size distribution scaling as $N_{max,rc} \propto r^{-2.65}$ (see the Appendix for the use of *DBH* or r in the tree-size distribution curve). The condition of full resource use would represent a state of maximum leaf area and biomass of the community. If this condition is met, then the slope of the size distribution curve is easily derivable ($N_{max,hc} \propto h^{-a(1+2H)}$). Thus any deviation of the size distribution curve in the real forest (observed) allows us to quantify the degree of forest disturbance. Indeed, if the community is somehow disturbed (i.e. it behaves as a "non-saturated

268 community") the competition among the individuals is less severe and the size
269 distribution curve is less steep.
270 Operationally, we used the Cumulative Distribution Function (CDF) for assessing the
271 tree-size distribution of the communities (Newman 2005). Generally, forestry studies
272 bin the diameters in size-classes, but it is necessary to choose the bin size (e.g. 2 or 5
273 cm) "a priori" and this subjective binning can affect the diameter distributions, the
274 regression and its exponent. We circumvented this hindrance by building a
275 Cumulative diameter-Distribution Function (CDF). The CDF describes the probability
276 of finding a diameter larger than each diameter considered. This probability is
277 calculated, after sorting all the diameters in ascending order, with the following
278 formula: $F_d=N_r/N_{tot}$, where N_{tot} is the total number of individuals measured in a given
279 plot and N_r is the rank of diameter *r*, i.e. the number of trees with a larger diameter
280 than any number of the sorted series. Notably, for mathematical reasons, the scaling
281 exponent of the CDF is equal to the predicted exponent for the Probability
282 Distribution Function (PDF) +1 (see Newman 2005). We then estimated the
283 distribution exponent with a linear regression of log CDF on log *r*,
284 Our <10 cm DBH tree dataset was representative for 800 m^2 of forest in each 1 ha
285 plot, so we multiplied the number of trees by 12.5. We thus obtained a dataset
286 representative for one ha of <10cm trees and merged it with the >10 cm DBH census
287 done by COBIMFO.
288 We conducted all analyses with the R-project software package.
289 **Results**
290 *Forest inventories*
291 The full inventories revealed a marked difference between the old-growth (MIX) and
292 regrowth-forest plots (JEU). Although the number of individuals greater than 10 cm

293 *DBH* was similar in all plots, there was a notable difference in the distribution of
294 small trees (*DBH* <10 cm) with the MIX plot hosting almost twice as many small
295 trees as the JEU plot (Table 1); the EDG plot had a similar number of small trees to
296 the MIX plot. Trees were markedly shorter in the most disturbed plot (JEU): the
297 tallest measured tree was 36 m in height compared to 55 to 60 m in the other two plots
298 (Table 1).

299 *Allometric scaling at individual level*

300 The scaling of V_{cro} with h did not differ among the three plots (Table 2) even though
301 the number of woody species was different (78 species in the MIX and 30 in the JEU).
302 The MIX plot showed an exponent of 3.36 (95%CI ±0.10), the EDG plot 3.30 (95%CI
303 ±0.09) and JEU 3.38 (95%CI ±0.12). Since H=1, $V_{cro} \propto h^{3a}$ implies a=1.12, 1.10 and
304 1.13 respectively. The most general exponent was obtained merging all the available
305 data leading V_{cro} to scale with h with an exponent of 3.34 (95%CI ±0.06),
306 corresponding to a = 1.11 (Fig. 1a).

307

308 We also tested whether other scaling relationships were species independent and/or
309 influenced by disturbances. The r_{cro} *vs*. h scaling returned similar exponents that did
310 not differ from 1.11 as also occurred in the scaling of l_{cro} with h (Table 2; Fig. 1b and
311 1c). This means that the scaling of the lateral expansion of the crown (r_{cro}) with crown
312 length (l_{cro}) is strictly isometric (i.e. H=1) in all species and plots.
313 The scaling between h *vs*. r showed a very small (but significant looking at the
314 confidence intervals) variation among plots with exponents of 0.74, 0.69 and 0.68 in
315 MIX, EDG and JEU plots respectively (Table 2 and Fig. 1d). When all data were
316 pooled, h scaled with r with a power of 0.71.

317

318 *Forest disturbance assessment*

319 The slope of the observed self-thinning line was estimated *only* considering the black
320 dots (i.e. within the cutoffs identified by the *H-model*), thus excluding 18% of trees in
321 the old-growth plot and 14 % of trees in the other two plots. The steepest self-thinning
322 line was measured in the MIX plot (-1.34) with the smallest difference compared to
323 the prediction (-1.65 dashed line) although this was significant (i.e. 95% CIs did not
324 include -1.65, Fig. 2a). The slope in the EDG plot was slightly less steep than the
325 MIX plot (-1.25) whereas that in the JEU plot (-0.99) was the least steep.

326

327 **Discussion**

328 Disturbance assessment is a fundamental requirement for implementing forest
329 protection policies and prioritizing restoration activities. Furthermore, numerous
330 ecological theories consider forest disturbance, which still has no standard assessment
331 approach (Asner 2013). Our results show that the slopes of tree-size distributions in
332 tropical forests of the Congo change with the degree of disturbance in agreement with
333 model expectations. Thus, by means of a minimum-effort inventory, a diagnostic tool
334 assessing forest disturbance can be implemented by simply comparing the slope of the
335 actual tree-size distribution with the potential slope predicted by the *H-model.* This
336 difference then represents a metric of forest disturbance related to functional
337 processes within the whole forest.

338

339 *Tree-level scaling relationships*

340 The V_{cro} *vs*. h scaling returns almost identical exponents in the three forests in spite of
341 structural and composition differences showing that the allocation trajectories are
342 genetically determined and are therefore site (i.e. plot) and disturbance independent.

343 Moreover, our study provides further evidence that the scaling of V_{cro} *vs.* h is nearly
344 species independent (Anfodillo et al. 2013) in forests growing at about the same
345 latitude. Indeed, comparing MIX and JEU, the composition changes are significant.
346 For instance, fully 69% of MIX species are not found in the JEU forest, and 24% of
347 JEU species are found only in the regrowth forest.

348 An additional in-depth analysis allows us also to include the possibility of a
349 hyper-allometric (i.e. >1) relationship among r_{cro} *vs.* h and also l_{cro} *vs.* h (Table 2).
350 We are thus able to further generalize the assumptions of the *H-model* by introducing
351 a new parameter "*a"*, which was not proposed in the model of Simini et al. (2010).
352 The parameter "*a*" could account for a scaling of V_{cro} with h larger than 3 (that would
353 be a geometrical limit) as in the Yangambi forest (e.g. 3.34). When r_{cro} and l_{cro} scale
354 with h with an exponent >1, crown radius and length increase slightly faster than
355 height with tree size, thus big trees will have a proportionally larger crown than small
356 ones.

357

358 *The slope of the "potential" tree-size distribution and its variations.*

359 The *H-model* predicts the slope of tree-size distributions under maximum resource
360 use: however in the less-disturbed plot (MIX) the difference between the predicted
361 and the empirical distribution was relatively large (Fig. 2a). There are two
362 explanations for this result. The most plausible is that forests are continuously
363 subjected to temporal and spatial disturbances (Wright 2005; Muller-Landau 2009;
364 Chambers et al. 2013), making the community seldom able to achieve a state for
365 maximally using the available resources. Indeed, the MIX forest is relatively close (<2
366 km) to very disturbed or deforested areas so it is plausible that some harvesting had
367 been done as suggested by the presence of *Pericopsis elata,* a light-demanding species

368 that regenerates in abandoned fields. Moreover, even natural processes might lead
369 towards "non-saturated conditions": for example, when a large tree falls and dies
370 younger plants might replace the whole leaf area lost (i.e. the amount of resources
371 used), but this process will need several years to be accomplished. Thus, there might
372 be a sort of "minimum background disturbance" that probably occurs because
373 growing processes in trees are relatively slow (years) compared to biomass losses
374 caused by disturbances (days) (Connell, 1978).

375 The second possible explanation is that the assumption of constant leaf density
376 with ontogenesis (i.e. B is proportional to V_{cro}) might be partially incorrect. Indeed, if
377 the self-shading of the leaves increases with tree size (Duursma et al. 2010), then B of
378 a single tree would increase less than V_{cro} and the scaling of V_{cro} would over-estimate
379 the slope of the tree-size distribution (i.e. *H-model* would predict a steeper fully
380 functional exponent than the real one). Since the total leaf area of a tree is very
381 difficult to precisely measure, especially in large trees, the isometry between B and
382 V_{cro} is an assumption to be further tested.

383 In summary, it may be possible to predict the potential tree-size distribution in
384 forests anywhere on the earth, regardless of species composition and disturbance just
385 by measuring how V_{cro} scales with h in some individuals of the area (e.g. even 100-
386 150 trees with the widest possible span of tree heights). Our approach could hence
387 leap over the "shifting baseline syndrome" (Vera, 2010; Ghazoul *et al*. 2015) without
388 needing any historical data or records of past disturbances and it might provide a
389 universal practical metric for addressing forest restoration and sustainable
390 management.

391

392 *Operationalizing forest disturbance.*

393 Forest disturbances include different events with different frequency, degree of
394 severity and rates of recovery, which all can differ in relation to ecosystem type. Thus,
395 it is challenging to find a simple tool for operationalizing (i.e. to measure) the general
396 term “disturbance”. However, our framework allows us to predict the slope of the
397 potential tree-size distribution and, consequently, provides a metric for quantifying
398 the degree of disturbance. Indeed, the steepest tree-size distribution curve (i.e. most
399 similar to the potential one) (Fig. 2a) was observed in the virtually undisturbed forest,
400 but the distribution diverged markedly in the JEU plot (Fig. 2c). In the EDG plot, the
401 slope was slightly less steep than the potential condition (Fig. 2b). The variation
402 between MIX and JEU plots in terms of degree of disturbance (the slope difference is
403 0.35) depicts an overall difference of 2441 individuals ha^{-1}, with the most notable
404 44% density reduction in small trees (<8.9 cm in diameter). However, we point out
405 that slope variations are only related to the proportion of individuals in the different
406 size-classes, and not to absolute stem density *per se*. For instance, we randomly
407 removed 2438 individuals from the inventory of the MIX plot, thus obtaining the
408 same stem density as in the JEU plot, and we fitted the new data. In spite of the
409 “artificial” exclusion of more than 1/3 of the individuals, the slope of the diameter
410 distribution did not change and we obtained the same slope as the original MIX
411 dataset (i.e. -1.34).

412 The EDG and MIX slopes differed slightly (difference of 0.09). Laurance et al.
413 (2006) showed artificial boundaries induced a reduction in stem density among larger
414 cohorts (>60 cm *DBH*) only 20 years after forest fragmentation in Amazonia. The
415 smaller cohorts should instead follow a “pulsating recruitment pattern” immediately
416 after the boundary establishment (Laurance et al. 1998; Laurance et al. 2011). Our
417 edge plot boundary was created about five years before sampling, so the EDG forest is

418 very likely in the pulsating phase reported by Laurance et al. (1998). The disturbance
419 might have increased the availability of resources (i.e. radiation) leading to less severe
420 competition among trees.

421 Awareness of finite-size scaling forces us to correctly estimate the slope of the
422 distribution only within the upper and lower cut-off (Fig 2). We suppose this might
423 have important consequences on the "stability" of the predictions. Indeed, other
424 authors assessed the degree of disturbance mainly by comparing biomass and
425 structure in subsequent inventories (e.g. Chave *et al*. 2008). However, episodic
426 mortality of large trees, which include a significant part of total biomass (Chambers *et*
427 *al.* 2013), might affect the results. For example, in the MIX plot, we estimate that the
428 5 largest trees account for more than 20% of the total biomass and the largest 100
429 trees (out of 6138) amount to about 75% of total biomass and 40% of total leaf area.
430 This dominance would explain why episodic disturbances to 8-10 trees, often the
431 biggest, could cause detectable variation in total biomass and create a sawtooth
432 pattern of biomass gain punctuated by occasional losses (Chambers *et al*. 2013). Our
433 approach behaves differently: the biggest trees are not *directly* used for estimating the
434 use of resources by the community because they are above the upper cut-off. For
435 example, in the MIX plot the upper cut-off is about 33 cm thus excluding about 130 of
436 the biggest trees. Undoubtedly, the presence of the large trees impacts on the number
437 of trees in the smaller cohorts because some resources are exploited, but we can
438 speculate that competition among all of them (which produces the tree-size
439 distribution) might, on average, be much less affected by the episodic losses of some
440 large trees.

441 As highlighted by Coomes et al. (2003) and Coomes & Allen (2007),
442 disturbances alter the expected tree-size distribution. Our data, and theory, suggest

443 that the slope of the tree-size distribution becomes flatter with more disturbance (as in
444 the JEU plot; Fig. 7). This is because when a disturbance causes tree mortality and
445 losses, resources become available for the remaining trees to exploit. Thus,
446 competition is generally lower in a sparse community leading to a flatter slope and the
447 size frequency distribution (within a diachronic approach) will be parallel to the X
448 axis (i.e. slope 0). Hence in our framework, after a disturbance event, the forest
449 approaches the slope of the "virtual steady state" coming from "above" (i.e. from -1.9
450 to -2.3) as reported also by Coomes *et al.* (2003) who found flatter slopes when the
451 finite size effect was excluded (trees <18 cm *DBH*) and Kerkhoff & Enquist (2007).
452
453 *Relevance for planning restoration activities*
454 We show that it is possible to predict "base-line" forest structure by measuring simple
455 traits, such as r_{cro}, l_{cro} and h. The independence of these variables from species and
456 disturbances might allow us to calculate the potential slope for all forests across the
457 globe, thus adding a quantitative tool for monitoring old-growth forest dynamics also
458 in temperate regions (Paillet et al. 2015). Furthermore, we show that the comparison
459 between the potential and observed slope provides a simple functional metric
460 depicting the degree of disturbance. This would allow us to prioritize restoration
461 activities simply by ranking all studied forests from the most to the least disturbed.
462 This ranking will be based on functional processes and not on subjective biomass
463 thresholds, which can vary among ecosystems.
464 The effectiveness of our minimum effort inventory (1-2 ha in tropical forests)
465 can be partially tested by comparing the results with other published data (even if the
466 finite size effect was, unfortunately, never considered in previous reports). Indeed, if
467 we consider the Yangambi MIX slope built with *DBH* values, without the finite-size

effect, we obtain a diameter distribution exponent of -1.06. This slope is relatively similar to the slopes reported by Muller-Landau *et al*. (2006) in Ituri-Edoro, about 450 km away and sharing many species with Yangambi, which ranged from -2.04 to -2.07 (so their CDF ranged from -1.04 to -1.07). Thus, Ituri trees' scaling of V_{cro} *vs.* h might be very similar to Yangambi trees'. This could mean that our medium-effort inventory may have a similar capacity in defining the forest structure as the 20 ha inventory used for Ituri-Edoro. It thus appears that it is possible to achieve a realistic representation of the forest structure with two 20x20m plots per ha for trees <10cm and a total inventory of trees >10cm *DBH* in 1 ha. Further tests will be necessary to fully demonstrate that our approach might overcome the necessity for measuring all trees in an area of at least 10 ha to detect forest disturbances in tropical forests (Chambers *et al.* 2013).

Conclusions

We propose a framework for predicting the structure (i.e. the slope of the tree-size distribution curve) of a virtually undisturbed forest built on metabolic scaling at the individual-level. This slope represents the general "baseline" for assessing the degree of disturbance in all forests. The application of our approach in three forests with different degree of disturbance shows how simple and effective the implementation of this metric can be. Thus, the *H-model* appears particularly suitable for implementation within the routine forest assessments. We emphasize that the importance of this tool for prioritizing forest protection and/or restoration activities in the tropics will be sorely needed in the coming years.

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Author Contributions: AT, MA and BJ originally formulated the idea. AT, BH and SG designed the experiment. SG, BM, DJ and HT conducted fieldwork. AT, SF and SG analysed the data. AT, SG, and BH wrote the manuscript. Other authors provided editorial advice.

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661 **Tables and Figures.**

662 *Table 1. Main structural parameters of the three sampled one hectare plots (all trees*

663 *>1.3 m in height) in the Yangambi region, Congo.*

664

Plot	Maximum Tree height (m)	Maximum *DBH* (cm)	Number of Individuals >10 cm (ha^{-1})	Number of individuals < 10 cm (ha^{-1})	Number of species (ha^{-1})
MIX	55	127.7	323	5815	78
EDG	60	157.0	456	5162	77
JEU	36	62.5	322	3250	30

665

666

667 *Table 2. Results of the regression analyses of V_{cro}, r_{cro}, l_{cro} vs. h and h vs. tree base*
668 *diameter (r) considering three plots in the Yangambi Region, Congo, under various*
669 *disturbance regimes separately (MIX, EDG and JEU).*

670

	Site	Intercept	Exponent	r^2	CI 95%	
$V_{cro} \sim h^{[a(1+2H)]}$					Intercept	Exponent
	MIX	0.0011	3.36	0.888	±0.0006	±0.10
	EDG	0.0018	3.30	0.896	±0.0011	±0.09
	JEU	0.0016	3.38	0.897	±0.0013	±0.12
$r_{cro} \sim h^{(aH)}$						
	MIX	0.092	1.11	0.844	±0.022	±0.04
	EDG	0.121	1.07	0.845	±0.03	±0.04
	JEU	0.083	1.14	0.866	±0.024	±0.05
$l_{cro} \sim h^{a}$						
	MIX	0.127	1.14	0.833	±0.033	±0.04
	EDG	0.12	1.16	0.825	±0.034	±0.04
	JEU	0.235	1.09	0.812	±0.08	±0.05
$h \sim r^{[2/(a(1+2H))]}$						
	MIX	160.8	0.74	0.924	±4.11	±0.02
	EDG	159.2	0.69	0.872	±4.98	±0.03
	JEU	167.3	0.68	0.902	±5.29	±0.03

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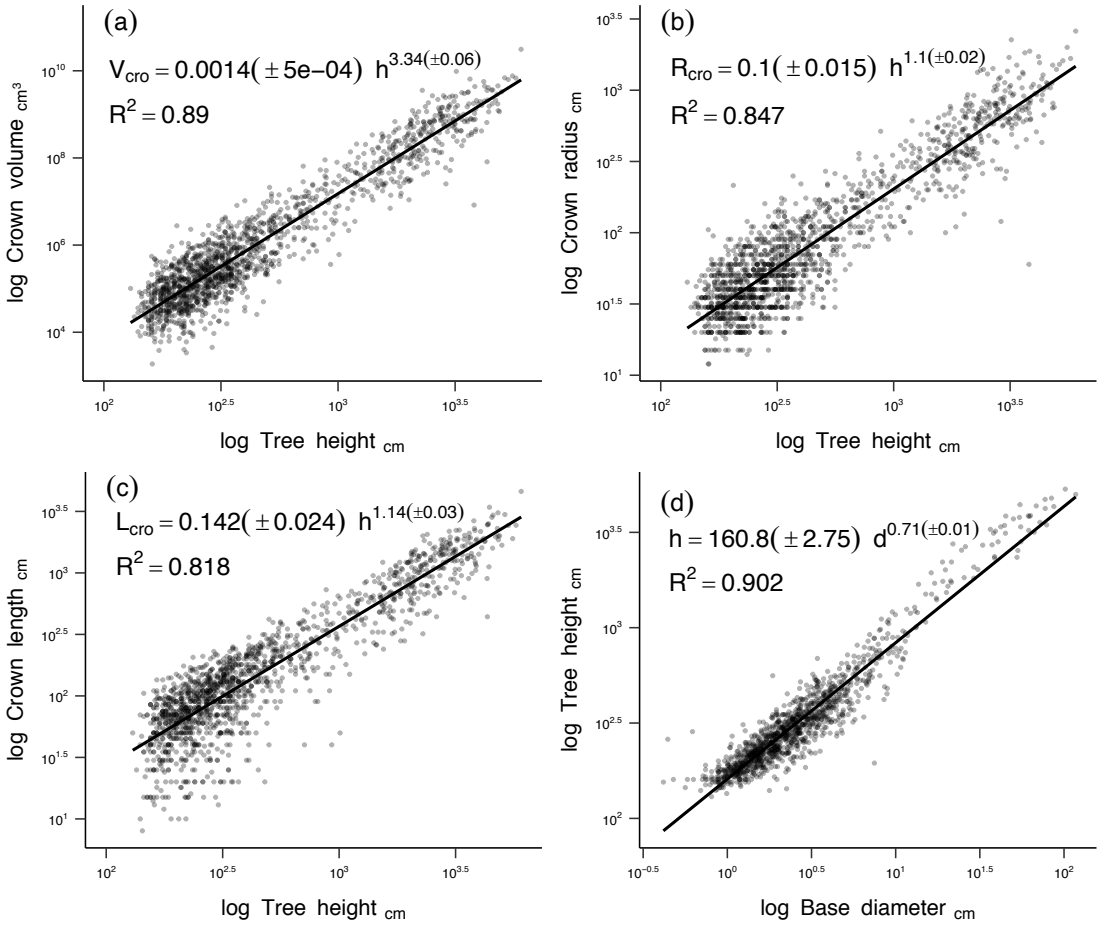
672

673 *Fig. 1. Scaling of (a) V_{cro} vs. h; (b) of r_{cro} vs. h; (c) l_{cro} vs. h; (d) h vs. r in three plots*
674 *of variously disturbed forest in Yangambi, The Congo (all data pooled together). In*
675 *parenthesis the ± 95% CI of the parameters*

676



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679 *Fig. 2. Cumulative Distribution Function (CDF) of base diameters (r). Grey dots*
680 *represent the upper and lower cut-off in the (a) MIX, (b) EDG, (c) JEU plot at*
681 *Yangambi, The Congo. The dashed line is the slope representing the "fully functional*
682 *forest". In parenthesis the ± 95% CI of the intercepts and slopes.*
683
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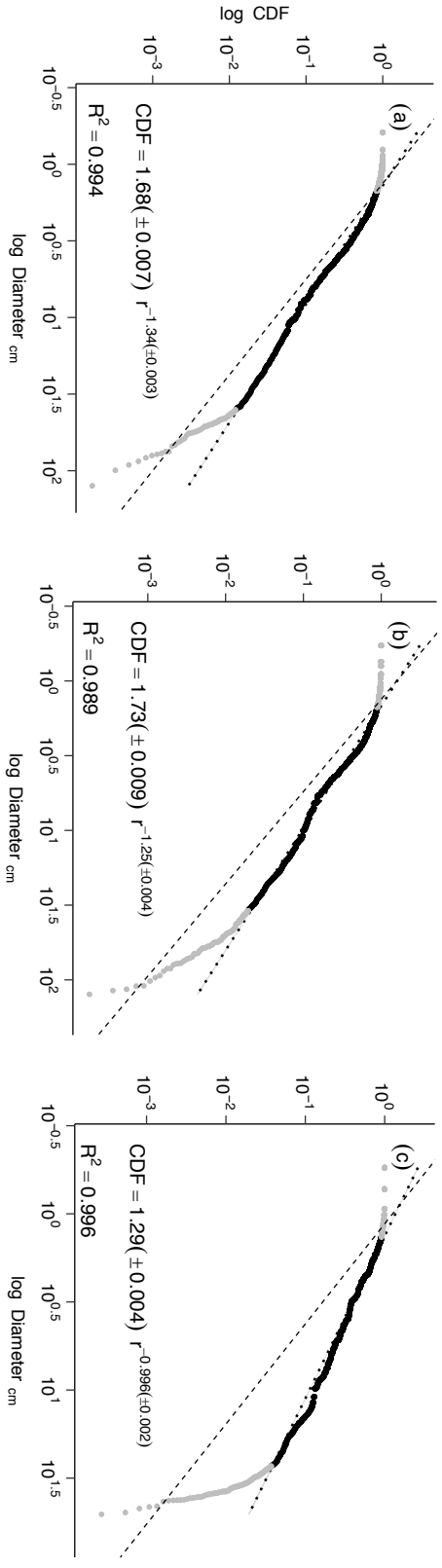
log CDF
(a)
CDF = 1.68(±0.007) r^-1.34(±0.003)
R^2 = 0.994
(b)
CDF = 1.73(±0.009) r^-1.25(±0.004)
R^2 = 0.989
(c)
CDF = 1.29(±0.004) r^-0.996(±0.002)
R^2 = 0.996
log Diameter cm

686

687